

Medial tines on the upper incisors and other dental features used as identification characters in European shrews of the genus *Sorex* (Mammalia, Soricidae)

By E. DANNEID

Department of Zoology, University of Stockholm

Receipt of Ms. 4. 1. 1988

Abstract

The accessory medial tines on the incisors are regarded as one of the best identification characters of shrews of the genus *Sorex*. This character is here described for all non-USSR European species of the genus, together with some other characters concerning pigment patterns, sharpness of cusps of I_1 , shape of A_1 , position of lacrimal and mental foramina and colour of pigment, all having some identification value. It is proposed that some of these characters reflect adaptive specializations rather than phylogenetic relationships. Finally a key to identification of species based on dental characters described in this paper is constructed.

Introduction

Species identification of shrew skulls has for European species of the genus *Sorex* mostly been based on the following characters: measurements of skulls and teeth, shape and size of upper antemolars (following REUMER [1984] the teeth more commonly called unicuspid are here termed antemolars) and position of mental foramen in the lower jaw.

Recently several authors on North American and East Asian shrews (HEPTNER and DOLGOV 1967; HOFFMANN 1971; HENNINGS and HOFFMANN 1977; DIERSING and HOFFMEISTER 1977; JUNGE and HOFFMANN 1981) have used the medial tines on the upper incisors as an effective identification character. The shape of the medial tines in European *Sorex* species has not previously been described in detail. Other characters, chiefly concerning pigment patterns, may also be used in identification. Some of these may be useful only for identification of certain species, while others are more generally applicable. It is possible to create a key to identification of European *Sorex* species using these characters, in some cases, however, combined with the position of the mental foramen, but without using the antemolars. This does not mean that the shape of the upper antemolars is a character of low identification value. Instead it is in most cases probably the easiest way to make an identification. However, using the "pigment-key" described here, it is also possible to identify specimens with damaged upper antemolars.

Material and methods

Skulls of nine shrew species of the genus *Sorex* were analyzed under a dissecting microscope. Geographical origin and number of skulls of each species is given in the table. The skulls were chiefly from young animals with teeth in good condition. (In old animals both the teeth and the pigment are worn to a considerable degree, which makes analyses difficult.) The following characters were studied: Presence or absence of medial tines on the upper incisors, their size and their position in the pigment field, pigmentation of hypocones on upper molars, position of lacrimal foramen, shape and pigmentation of the lower incisor, shape of the lower antemolar, pigment pattern on I_1 - P_4 , position of mental foramen and colour of the pigment.

Geographical origin and number of skulls studied of each species

Species	Number of skulls	Geographical area	Source
<i>S. alpinus</i>	28	Switzerland, Germany, Yugoslavia	1, 3
<i>S. araneus</i>	20	Sweden, Finland, Germany, Czechoslovakia	1
<i>S. caecutiens</i>	36	Sweden, Finland	1, 2
<i>S. coronatus</i>	26	Switzerland	3
<i>S. granarius</i>	13	Spain	3
<i>S. isodon</i>	31	Finland	2
<i>S. minutissimus</i>	8	Finland	2
<i>S. minutus</i>	28	Sweden, Germany	1
<i>S. samniticus</i>	15	Italy	3

Source: 1 = Swedish Museum of Natural History, Stockholm, Sweden; 2 = University of Oulu, Finland; 3 = Université de Lausanne, Switzerland.

Note: Apart from these forms, four additional species occur in the European part of USSR, *S. tundrensis* in the Pechora River valley etc. and the three Caucasian species *S. caucasicus*, *S. raddei* and *S. volnuchini*.

Results

Subgeneric characters

According to HALL (1981) and JUNGE and HOFFMANN (1981) the majority of North American *Sorex*-species can be divided into the two subgenera *Sorex* and *Otisorex* (*Microsorex* is a monotypic subgenus characterized by the reduction of the third upper antemolar and will not be considered further.) The subgenus *Sorex* is characterized by the presence of a post-mandibular canal and by the absence of a pigmented ridge on the upper antemolars, *Otisorex* is conversely characterized by the opposite combination: absence of a post-mandibular canal and presence of a pigmented ridge on upper antemolars. No European *Sorex* showed any trace of a pigmented ridge on the upper antemolars. A postmandibular canal was present on at least one side (mostly on both), except in three skulls (one *S. coronatus* and two *S. samniticus*). The conclusion is that all European *Sorex* species belong to the subgenus *Sorex*.

Shape of upper incisors (frontal view)

The presence of accessory medial tines on the upper incisors (Fig. 1) was first noted by HEPTNER and DOLGOV (1967) in the East Asian species *S. mirabilis*. They "proposed a new subgenus, *Ognevia* to accomodate what they believed to be important peculiarities found in *S. mirabilis*" (citation from HOFFMANN 1971). Since then it has been found that medial tines occur in many species of *Sorex* and that their presence or absence, size and position in the pigmented field is a very good identification character (DIERSING and HOFFMEISTER 1977; HENNINGS and HOFFMANN 1977; JUNGE and HOFFMANN 1981). Another character, closely related to the shape of the medial tines is the shape of the tips of the incisors and their specing relative to each other. If the medial tines were situated low in the pigmented zone the free incisor tips (the area below the medial tines) were consequently short and also mostly parallel. However, if the tines were situated high up, the incisor tips were long and usually somewhat diverging.

In frontal view the first pair of upper antemolars may be more or less visible behind the incisors. They are clearly visible in *S. alpinus* and *S. samniticus*, less so in other species. Finally the colour of the pigment, how high the pigmented area rises on the incisor and if the upper border of the pigmented area on the first cusp on I¹ is straight or oblique may all be worth noticing.

Sorex araneus (Fig. 1a): Pigment dark, medial tines rather large, situated in the lower half of the pigmented area (sometimes as high as at the middle of this area), tips of incisors blunt, parallel, not diverging.

Sorex coronatus: Not distinguishable from *S. araneus*.

Sorex granarius (Fig. 1b): Pigment rather light, medial tines small to very small, situated in the lower half of the pigmented area, tips of incisors similar to *S. araneus*.

Sorex samniticus (Fig. 1c): Pigment intermediate, medial tines large, situated in the upper half of the pigmented area, tips of incisors were slightly more diverging than in most *S. araneus*.

Sorex caecutiens (Fig. 1d): Colour of pigment intermediate between *S. araneus* and *S. minutus*, medial tines very small to fairly large, usually situated near the middle of the pigmented area (but sometimes fairly deep in the lower half), tips of incisors diverging,

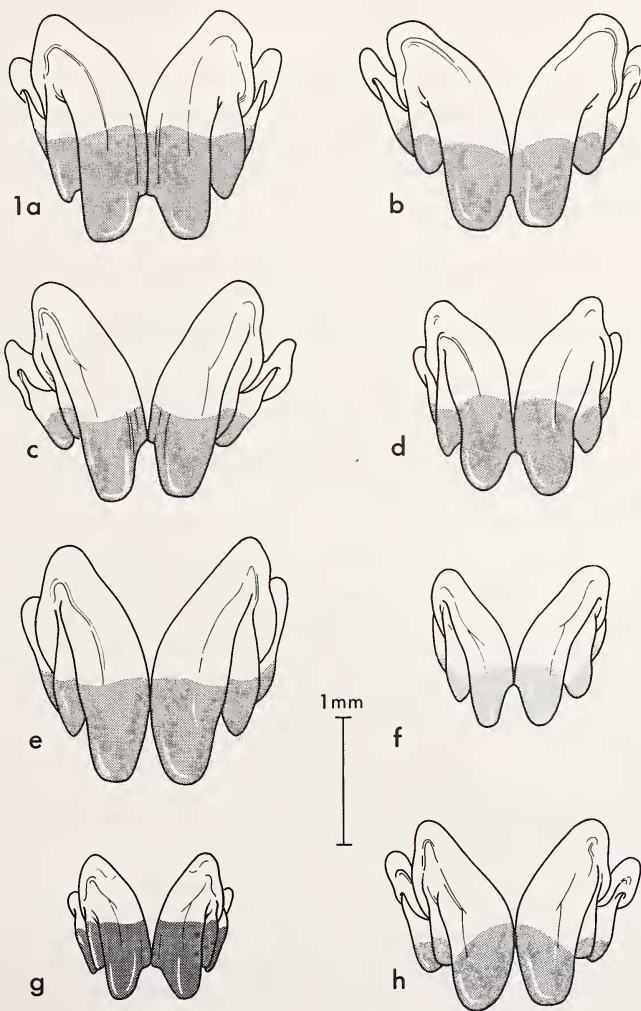


Fig. 1. Upper incisors of shrews in frontal view. a: *S. araneus*; b: *S. granarius*; c: *S. samniticus*; d: *S. caecutiens*; e: *S. isodon*; f: *S. minutus*; g: *S. minutissimus*; and h: *S. alpinus*

rather sharp-pointed, upper borderline of pigmented area straight to oblique (see *S. alpinus*).

Sorex isodon (Fig. 1e): Pigment intermediate, medial tines very small, situated in the uppermost part of the pigmented area, tips of incisors blunt, rather parallel to slightly diverging.

Sorex minutus (Fig. 1f): Pigment light, medial tines rather large, situated in the upper half of the pigmented area, tips of incisors more sharp-pointed and diverging than in any other species.

Sorex minutissimus (Fig. 1g): Pigment very dark, medial tines very large, situated extremely low in the pigmented area, which made the tips of the incisors very short and rather blunt. This was the only species where the pigment cover rose as high as the dividing point between the first and second cusp of the incisor. It was also unique in that a small area of lighter pigment separated the pigmented and nonpigmented areas. These facts together with the elongated shape of the incisor makes *S. minutissimus* one of the easiest species to recognize.

Sorex alpinus (Fig. 1h): Pigment rather light, medial tines absent, tips of incisors blunt and parallel to slightly diverging. In this species the upper borderline of the pigmented area was clearly oblique, while in all other species it was relatively straight (some *S. caecutiens* had a borderline almost as oblique as *S. alpinus*). In frontal view the first antemolar was clearly visible behind the incisors in this species, a condition also found in *S. samniticus* but not in other European *Sorex* species.

Pigmented hypocones on upper molars

This character (Fig. 2) separates *S. araneus* and *S. coronatus* from all other species. In young *S. araneus* and *S. coronatus* the hypocones on M¹ and (usually) M² (and very rarely P⁴ as well) were very weakly pigmented (in old animals the teeth are worn, and naturally the pigment on the hypocones is absent), while in all other species (even the related *S. granarius*) the hypocones were completely unpigmented.



Fig. 2. Left M¹ of *S. araneus* showing pigmented hypocone (arrow)

Relative position of lacrimal foramen

Although not being of the same importance as the position of the mental foramen, the position of the lacrimal foramen relative to the first and second upper molar teeth is sometimes a useful taxonomic character (VAN ZYLL DE JONG 1980). Lacrimal foramen placed over:

1. central part of M¹ (mesostyle to between metacone and metastyle): *S. araneus*, *S. coronatus*, *S. granarius*, *S. samniticus*, *S. caecutiens*.
2. posterior part of M¹ (metacone to metastyle): *S. minutus*, *S. minutissimus*, *S. isodon*.
3. between M¹ and M² or over parastyle of M²: *S. alpinus*.

Shape of I₁

The shape of the lower incisor can in some cases be used to distinguish between species. Characters worth noticing are the shape and size of the cusps and the distribution of the pigmented area (Fig. 3). All European *Sorex* species had four cusps, but there was a great difference between the sharp, triangular cusps of *S. minutus* and the blunt, rounded cusps of *S. araneus*. *S. minutissimus* also had a clearly recognizable cusp-pattern. *S. minutus* was

the only species showing really sharp-pointed cusps; while several species (*S. granarius*, *S. samniticus* and *S. alpinus*) had blunter cusps than *S. araneus*.

The relative size of the cusps may also be important. The third cusp was mostly larger, often considerably so, than the fourth. However, in *S. minutus* and *S. alpinus* the third and fourth cusps were of approximately the same size, even though the fourth appeared smaller because it was less pigmented.

In labial view the pigment on the lower part of the tooth reached backwards to a point approximately between first and second cusps in most species, while in *S. minutissimus* it reached further back, between the second and third cusps, which simply means that I_1 had a larger pigmented area in this species. In *S. minutus*, *S. minutissimus*, *S. alpinus*, *S. granarius* and *S. samniticus* all four cusps were usually included in a continuous pigmented area, while in *S. araneus* and *S. coronatus* the pigment of the fourth cusp were often isolated from the main pigmented area. In *S. caecutiens* and *S. isodon* the third cusp were also sometimes isolated in this way.

Shape of A_1

In *S. araneus* and *S. coronatus* this tooth was more or less triangular in shape, while in other species it was prolonged and sometimes showed a prominent posterior ridge (Fig. 3). This ridge was usually unpigmented but in some species (*S. minutus*, *S. minutissimus*, *S. samniticus*) it was sometimes pigmented. In *S. alpinus* the ridge was pigmented and transformed into a cusp, which gave this species a two-cusped A_1 . It is often stated that *S. alpinus* is the only European *Sorex* showing this condition, however, specimens of both *S. samniticus* and *S. minutissimus* with a two-cusped A_1 were found. In these cases the second cusp was much smaller than and closer to the first cusp compared with what was found in *S. alpinus* (Fig. 3c-d).

Pigment pattern on I_1 - P_4

The border between the pigmented and unpigmented areas of the first three teeth in the lower jaw is sometimes useful for distinguishing species. Three patterns can be recognized:

1. The "araneus-pattern" (Fig. 3a): The border between pigmented and unpigmented areas runs continuously on I_1 , A_1 and P_4 , without apparent breaks. This condition was found in *S. araneus* and *S. coronatus*.
2. The "minutus-pattern" (Fig. 3b): The border between pigmented and unpigmented areas runs continuously on I_1 and A_1 but probably due to the non-triangular shape of the latter tooth, starts much higher on P_4 , leaving a distinct gap. This condition was found in *S. minutus*. In *S. granarius*, *S. samniticus*, *S. caecutiens*, *S. isodon* and *S. minutissimus* the pattern was often somewhat intermediate between the two patterns described above.
3. The "alpinus-pattern" (Fig. 3d): The border between pigmented and unpigmented areas runs continuously on I_1 and A_1 but on P_4 it starts much lower, almost from the basal part of the tooth, and then runs in a semi-circular fashion over P_4 . This was found only in *S. alpinus*.

Relative position of mental foramen

The position of the mental foramen relative to P_4 - M_1 is commonly used in field guides etc. but not always accurately. In this study the following positions were found (Fig. 3):

S. alpinus: below P_4 or sometimes below P_4 - M_1 .

S. isodon: below P_4 - M_1 or below the anterior part of the trigonid of M_1 , seldom centrally placed below the trigonid of M_1 .

S. minutus: below the anterior part of the trigonid of M_1 .

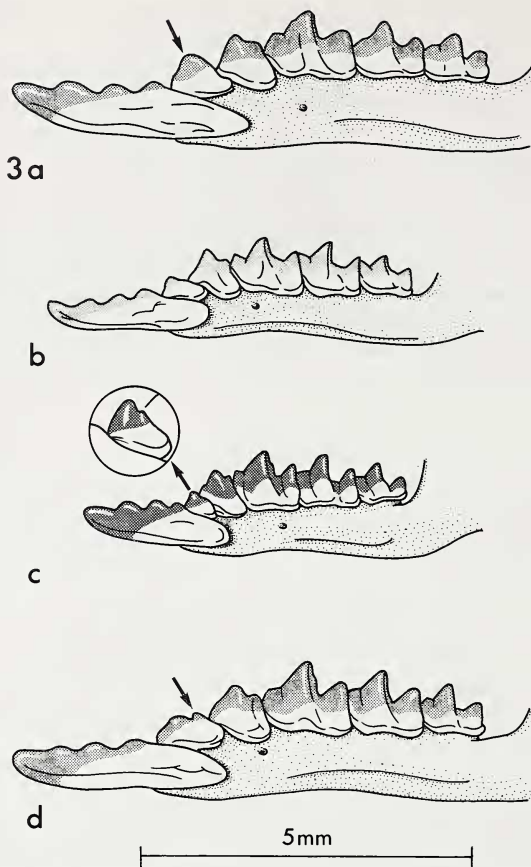


Fig. 3. Left lower jaw of shrews in labial view; a: *S. araneus* showing triangular A_1 (arrow) and typical „araneus“-pigment pattern on I_1 - P_4 ; b: *S. minutus* showing sharp cusps on I_1 and typical „minutus“-pigment pattern on I_1 - P_4 ; c: *S. minutissimus* (and inserted a two-cusped A_1 which is not normal for the species); d: *S. alpinus* showing a two-cusped A_1 (arrow) and „alpinus“-pigment pattern on I_1 - P_4 . The mental foramen is visible under P_4 - M_1

S. araneus, *S. coronatus*, *S. caecutiens*, *S. granarius* and *S. samniticus*: below the trigonid of M_1 , relatively centrally placed.

S. minutissimus: below the trigonid-talonid of M_1 .

Colour of pigment

The colour (actually the degree of darkness/lightness) of the pigment has already been reviewed in the section dealing with the upper incisors. What is said there is also true for the pigment generally, *S. minutus* has the lightest pigment, *S. minutissimus* the darkest and the other species are intermediate. It should be borne in mind that the pigment is generally darker on the lower incisor than further back in the lower jaw.

The red colour of the pigment is due to the presence of iron (DÖTSCH and VON KOENIGSWALD 1978; VOGEL 1984). According to DÖTSCH and VON KOENIGSWALD (1978) the lower incisor shows the greatest quantity of iron in *S. araneus*. The same may be true for most species of *Sorex*.

Discussion

The medial tines on the upper incisors are a good specific identification character. The question is, however, if similarities in the characters described in this work reflect taxonomic relationships between species or are results of adaptations to a similar way of life. The parallelism may occur is demonstrated by the two smallest species in the Old and New World, *S. minutissimus* and *S. (Microsorex) boyi* respectively. Seen in frontal view the incisors of these two pygmy species are very similar (c.f. Fig. 1g in this work and Fig. 4 in JUNGE and HOFFMANN 1981), with their large medial tines placed low down on the teeth and their very dark pigment. The front part of the jaw is shortened in both species, but the effect of this shortening on the upper antemolars is quite distinct in the two forms. In *S. boyi* the third and the fifth antemolars are reduced so that the animal at a quick glance appears to have only three upper antemolars. In *S. minutissimus* all five antemolars are well-developed but situated close together. Since these species are not closely related, these similarities must be adaptations to a similar way of life.

The best available evidence for phylogenetic relationships between European *Sorex* is probably cytological. Of the nine species described in the present paper, three (*S. araneus*, *S. coronatus* and *S. granarius*), belong to the *Sorex araneus/arcticus*-group, characterized by two-armed x-chromosomes and (in males) two y-chromosomes (HAUSSER et al. 1985). *S. samniticus*, although superficially similar has a completely different karyotype (GRAF et al. 1979) and is also electrophoretically different (CATZEFLIS, thesis 1984). It is interesting to note that *S. araneus*, *S. coronatus* and *S. granarius* all have medial tines situated in the lower half of the pigmented area while *S. samniticus* has them in the upper part. However, this does not amount to state that the *S. araneus/arcticus*-group is characterized by medial tines located in the lower part of the pigmented field of the incisors. Firstly the shape of the medial tines is not known in Asian members of this group, and the North American forms have, as indicated by JUNGE and HOFFMANN (1981 p. 20) the medial tines high on the anterior face of I¹. Secondly many other species (in Europe *S. minutissimus*) have medial tines placed low on the incisors.

Even though the phylogenetic value of some characters mentioned in this work seems to be limited, the characters uniting *S. araneus* and *S. coronatus* (pigmented hypocones on M¹-M², perhaps also the triangular A₁) appear to confirm that these species are closely related.

If the characters mentioned are instead regarded as ecological adaptations the question arises: to what? What does it mean for example if a shrew has dark or light tooth pigment?

As the pigment is iron-containing, teeth with dark pigment are probably more resistant to wear. It is generally agreed that wear of teeth in shrews is chiefly accomplished by chewing. The shrew dentition comprises two functional parts: a front part containing incisors and antemolars and a back part consisting of the molariform teeth (DÖRSCH 1985; MALMQUIST, pers. comm.). The front part chiefly functions as a pair of tweezers when the shrew is catching the prey, while the back part is involved in chewing. Catching the prey probably causes less wear than chewing it. Still, the lower incisor is the most heavily pigmented tooth at least in *S. araneus* (DÖRSCH and VON KOENIGSWALD 1978). Could there be any other use for heavily pigmented incisors apart from dealing with sclerotized invertebrates?

It is well known that many species of shrews spend much time underground in burrows, self made or (for smaller species like *S. boyi*) even insect-tunnels. If the incisors are involved in removing stones etc. from tunnels (CROWCROFT 1957) it would obviously be valuable to have heavily pigmented incisors. It might also be advantageous to have large medial tines placed very low on the incisors to provide a more efficient digging apparatus (compare fig. 1a and 1f). If this is true, we would expect a correlation between dark

pigment and large medial tines located low on the incisors. This might be true because *S. araneus* has darker pigment than *S. minutus* and also medial tines situated lower.

S. minutissimus has the largest (at least in relative size) and lowest positioned medial tines of all species and also the darkest pigment. It is also true that *S. araneus* spends more time underground than *S. minutus* (CROIN MICHELSEN 1966). It should be expected that *S. minutissimus* has an even more subterranean behaviour.

The only species showing extensive variability in position of medial tines was *S. caecutiens*. Out of 36 skulls, 28 showed medial tines situated at the middle of the pigmented area or a little below, while 5 had the medial tines placed low in the pigment (the remaining 3 had damaged incisors). This may be due to the fact that *S. caecutiens* is an intermediate form also in body size. The Scandinavian species are ranked in order of decreasing size as follows: *S. isodon* – *S. araneus* – *S. caecutiens* – *S. minutus* – *S. minutissimus*. In the extremes *S. isodon* and *S. minutissimus* no variation at all could be observed in medial tines, and in *S. araneus* and *S. minutus* the variation was only minute. Having intermediate size, *S. caecutiens* could perhaps occupy the niche of *S. araneus* in absence of that species, while in the presence of *S. araneus* but absence of *S. minutus* it could tend so shift to the niche of *S. minutus* as suggested by HANSKI and KUITUNEN (1986). This might produce variation in the position of the medial tines. It might be argued that considerable intraspecific variation in the position of the medial tines renders this character useless as a systematic character, however, in no other species was there any significant variation.

S. minutus has sharp cusps on the lower incisor, while those of *S. sinalis*, *S. caecutiens* and *S. minutissimus* are blunter, those of *S. araneus* and *S. coronatus* still blunter and those of *S. granarius*, *S. samniticus* and *S. alpinus* finally extremely low and blunt. There is much more individual variation in this character than in the position of medial tines, which may be due to tooth wear.

One observation that might be of ecological importance is that *S. minutus* shows much sharper cusps on I_1 than any other European *Sorex*. This is probably not due to dealing with more chitinized prey than other species, since this is contradicted by the light pigment of the teeth. According to PERNETTA (1976), *S. minutus* ate adult Coleoptera, Opiliones, Araneae and larvae (in that order) while the more blunt-cusped *S. araneus* ate earthworms, adult Coleoptera and Opiliones, and only to a lesser degree larvae and spiders. *S. minutus* does not eat earthworms which form a large part of the diet of *S. araneus* (CHURCHFIELD 1984). The sharp cusps on I_1 of *S. minutus* may give a better hold on to the prey during the capture. *S. minutus* does not do much digging and may therefore maintain sharper cusps on I_1 than for example, *S. araneus*.

Key to identification of species

1. Unpigmented hypocones on M^1 – M^2 (Fig. 2), A_1 not triangular (Fig. 3b–d) 2
- 1a. Pigmented hypocones on M^1 – M^2 (Fig. 2), A_1 triangular (Fig. 3a)
 *S. araneus*/*S. coronatus* (not distinguishable using this key)
2. Medial tines present on I^1 (may be small), upper border of pigment on I^1 seen in frontal view mostly straight, A_1 one-cusped, not “alpinus-pigment pattern” on I_1 – P_4 3
- 2a. Medial tines on I^1 absent (Fig. 1h), upper border of pigment on I^1 seen in frontal view clearly oblique, A_1 two-cusped (*S. samniticus* and *S. minutissimus* might rarely have a two-cusped A_1 but it looks different, see Fig. 3c), “alpinus-pigment pattern” on I_1 – P_4 (Fig. 3d) *S. alpinus*
3. Medial tines on I^1 in upper half of pigmented area 4
- 3a. Medial tines on I^1 in lower half of pigmented area 7
4. Mental foramen under the middle of the trigonid of M_1 5
- 4a. Mental foramen more anteriorly 6

5. Tips of incisors parallel, medial tines mostly high up in the pigmented area (Fig. 1c) *S. samniticus*
- 5a. Tips of incisors diverging, medial tines mostly near the middle of the pigmented area (Fig. 1d) *S. caecutiens*
6. Pigment darker, medial tines small, tips of incisors rather parallel, blunter, cusps on I₁ rather blunt (Fig. 1e) *S. isodon*
- 6a. Pigment lighter, medial tines rather large, tips of incisors diverging, sharper, cusps on I₁ sharp (Fig. 1f) *S. minutus*
7. Pigment very dark, medial tines on I¹ large (Fig. 1g) *S. minutissimus*
- 7a. Pigment light, medial tines on I¹ not very large 8
8. Tips of incisors more parallel, medial tines clearly in the lower half of the pigmented area (Fig. 1b) *S. granarius*
- 8a. Tips of incisors more diverging, medial tines mostly near the middle of the pigmented area, only rarely further below (Fig. 1d) *S. caecutiens*

Note: The difference between 8 and 8a is very slight when *S. caecutiens* has low placed medial tines but since the two species occur in widely separated geographical areas the risk for confusion should seldom occur.

Acknowledgements

I wish to express my gratitude to the Swedish Museum of Natural History, to Prof. SEPPÖ SULKAVA, Oulu, and to Prof. JACQUES HAUSSER, Lausanne for loaning me the material. I also wish to thank Prof. BO FERNHOLM, Stockholm, Dr. LARS WERDELIN, Stockholm and Dr. MATS MALMQUIST, Uppsala for critical comments on the manuscript. Finally I wish to thank Ms. BIBBI MAYRHOFER for helping me with the illustrations.

Zusammenfassung

Mediale Pfeiler an den oberen Schneidezähnen und andere Zahnmerkmale als Hilfe bei der Bestimmung europäischer Spitzmäuse der Gattung Sorex (Mammalia, Soricidae)

Die akzessorischen medialen Pfeiler (accessory medial tines) an den oberen Schneidezähnen gelten als wichtiges Merkmal zur Bestimmung von Spitzmäusen der Gattung *Sorex*. Dieses Merkmal wird hier an allen neun Arten untersucht, die in Europa außerhalb von Rußland vorkommen. Außerdem werden Verteilung und Intensität des Zahnpigments, die Gestalt der beiden Zähne I₁ und A₁ im Unterkiefer, die Lage des Foramen lacrimale und des Foramen mentale beschrieben. Die adaptive Bedeutung dieser Merkmale wird diskutiert. Ein auf diesen Kennzeichen aufbauender Bestimmungsschlüssel für die neun *Sorex*-Arten wird angegeben.

References

- CHURCHFIELD, S. (1984): Dietary separation in three species of shrew inhabiting water-cress beds. *J. Zool. London* 204, 211–228.
- CROIN MICHELSEN, N. (1966): Intraspecific and interspecific competition in the shrews *Sorex araneus* and *S. minutus* L. *Archives Néerlandaises de Zoologie* 17, 73–174.
- CROWCROFT, P. (1957): *The life of the shrew*. London: Stellar Press.
- DIERSING, V. E.; HOFFMEISTER, D. F. (1977): Revision of the shrews *Sorex merriami* and a description of a new species of the subgenus *Sorex*. *J. Mammalogy* 58, 321–333.
- DÖTSCH, C. (1985): Masticatory function in shrews (Soricidae). *Acta Zool. Fennica* 173, 231–235.
- DÖTSCH, C.; v. KOENIGSWALD, W. (1978): Zur Rotfärbung von Soricidenzähnen. *Z. Säugetierkunde* 43, 65–78.
- GRAF, J.-D.; HAUSSER, J.; FARINA, A.; VOGEL, P. (1979): Confirmation du statut spécifique de *Sorex samniticus* Altobello, 1926 (Mammalia, Insectivora). *Bonner Zool. Beitr.* 30, 14–21.
- HALL, E. R. (1981): *The mammals of North America*. 2nd ed. New York: Wiley.
- HANSKI, I.; KUITUNEN, J. (1986): Shrews on small islands: epigenetic variation elucidates population stability. *Holarctic ecology* 9, 193–204.
- HAUSSER, J.; CATZEFLIS, F.; MEYLAN, A.; VOGEL, P. (1985): Speciation in the *Sorex araneus* complex (Mammalia: Insectivora). *Acta Zool. Fennica* 170, 125–130.

- HENNINGS, D.; HOFFMANN, R. S. (1977): A review of the taxonomy of the *Sorex vagrans* species complex from western North America. Occ. paps. Mus. nat. hist. Univ. Kansas **68**, 1–35.
- HEPTNER, V. G.; DOLGOV, V. A. (1967): O sistematicheskom polozhenii *Sorex mirabilis* Ognev, 1937 (Mammalia, Soricidae). Zool. Zhur. **56**, 1419–1422.
- HOFFMANN, R. S. (1971): Relationships of certain Holarctic shrews, genus *Sorex*. Z. Säugetierkunde **36**, 193–200.
- JUNGE, J. A.; HOFFMANN, R. S. (1981): An annotated key to the longtailed shrews (genus *Sorex*) of the United States and Canada, with notes on Middle American *Sorex*. Occ. paps. Mus. nat. hist. Univ. Kansas **94**, 1–48.
- PERNETTA, J. C. (1976): Diets of the shrews *Sorex araneus* L. and *Sorex minutus* L. in Wytham grasslands. J. Anim. Ecol. **45**, 899–912.
- REUMER, J. W. F. (1984): Ruscian and early pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (the Netherlands) and Hungary. Scripta Geol. **73**, 1–173.
- VAN ZYLL DE JONG, C. G. (1980): Systematic relationships of woodland and prairie forms of the common shrew, *Sorex cinereus cinereus* Kerr and *S. c. haydeni* Baird in the Canadian prairie provinces. J. Mammalogy **68**, 66–75.
- VOGEL, P. (1984): Verteilung des roten Zahnschmelzes im Gebiß der Soricidae (Mammalia, Insectivora). Rev. suisse Zool. **91**, 699–708.

Author's address: ERLAND DANNEID, Department of Zoology, University of Stockholm, S-106 91 Stockholm, Sweden